

Simulated nitrogen cycling response to elevated CO₂ in *Pinus taeda* and mixed deciduous forests

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Summary Interactions between elevated CO₂ and N cycling were explored with a nutrient cycling model (NuCM, Johnson et al. 1993, 1995) for a *Pinus taeda* L. site at Duke University, North Carolina, and a mixed deciduous site at Walker Branch, Tennessee. The simulations tested whether N limitation would prevent growth increases in response to elevated CO₂, and whether growth responses to CO₂ in N-limited systems could be facilitated by increasing the biomass/N ratio (reducing N concentration) or increasing litter N mineralization, or both.

Nitrogen limitation precluded additional growth when target growth rates and litterfall were increased (simulating potential response to elevated CO₂) at the Duke University site. At the Walker Branch site, increasing target growth and litter-fall caused a 7% increase in growth. Reducing foliar N concentrations reduced growth because of N limitation created by reduced litter quality (C:N ratio), reduced decomposition and increased N accumulation on the forest floor. These effects were most pronounced at the Duke University site, because the forest floor N turnover rate was lower than at the Walker Branch site. Reducing wood N concentration allowed prolonged increases in growth because of greater biomass/N; however, N uptake was reduced, allowing greater N immobilization on the forest floor and in soil. Increased N mineralization caused increased growth at the Duke University site, but not at the Walker Branch site.

These simulations pose the counterintuitive hypothesis that increased biogeochemical cycling of N (as a result of increased litterfall N) causes reduced growth in an N-limited system because of increased accumulations of N on the forest floor and in soil. Translocation of N from senescing leaves before litterfall mitigates this response by allowing the trees to retain a greater proportion of N taken up rather than recycle it back to the forest floor and soil where it can be immobilized. Eliminating N translocation at Walker Branch changed the direction as well as the magnitude of the responses in three of the four scenarios simulated. Because the NuCM model does not currently allow translocation in coniferous species, the effects of translocation on N cycling in the Duke University simulations are not known.

Keywords: biogeochemical cycling, C:N ratio, loblolly pine, N immobilization, N mineralization, nutrient cycling model, translocation.

Introduction

The long-term effects of elevated CO₂ on growth and C sequestration are highly dependent on the availability and cycling of other elements such as N. Elevated CO₂ can mitigate mineral nutrient deficiencies by promoting either nutrient uptake or biomass production per unit of nutrient uptake, or both, especially in the case of N (Zak et al. 1993, McGuire et al. 1997, Johnson et al. 1997, 1998a). On the other hand, elevated CO₂ can exacerbate nutrient deficiencies by introducing high C/nutrient ratio litter and labile organic compounds into the soil, which cause immobilization of nutrients, especially N (Strain 1985, Diaz et al. 1993). Many of these nutrient mobilization-immobilization processes have been studied in detail in isolation from the ecosystem; however, the feedbacks among these processes are numerous and complicated, and currently there is no consensus on how they will modify the long-term effects of elevated CO₂ on growth and C sequestration.

In a series of ecosystem-level experiments in the Arctic tundra of Alaska, Shaver et al. (1992) found no long-term response to either elevated CO₂ or increased irradiance, because of limited nutrient availability (N and P). Shaver and his colleagues proposed that long-term ecosystem productivity and carbon cycling can be affected significantly only through actions on nutrient cycles. McKane et al. (1997) simulated the field experiments described by Shaver et al. (1992) by means of the Marine Biological Laboratory-Global Ecosystem Model (MBL-GEM), and found that increased biomass in response to elevated CO₂ in these ecosystems can be attributed solely to an increase in plant tissue C:N ratio.

Simulations employing the Multiple-Element Limitation (MEL) model (Rastetter et al. 1997) indicated that the short- and long-term responses of a northern hardwood forest to elevated CO₂ were controlled by different N cycling processes at four time scales: (1) an instantaneous response associated with an increase in vegetation C:N ratio; (2) a response over a period of years facilitated by greater N uptake, because of greater allocation of resources to uptake; (3) a net movement of N from soils (low C:N ratio) to vegetation (high C:N ratio) over a period of decades; and (4) accumulation of N in the ecosystem over a period of centuries.

I have explored some of the potential feedbacks that elevated CO₂ can cause in forest nutrient cycles with the Nutrient

Cycling Model (**NuCM**) (Johnson et al. 1993, 1995). The **NuCM** considers nutrient cycling processes on a smaller (stand-level) scale than the models described above and includes detailed and complex soil chemical components. Thus, although **NuCM** may be too complex to be used on a regional or global scale, it can be used to identify important processes that ought to be included in more general models.

The Nutrient Cycling Model

The Nutrient Cycling Model (**NuCM**) was developed primarily to explore the effects of atmospheric deposition, fertilization, and harvesting in forest ecosystems (Johnson et al. 1993, 1995). It is a stand-level model incorporating all major nutrient cycling processes (uptake, translocation, leaching, weathering, organic matter decay, and accumulation). The model simulates the cycling of N, P, K, Ca, Mg, and S based on expected (target) growth rates (input by the user and reduced in the event of nutrient limitation), user-defined litterfall rates, and weathering, N and S mineralization rates, soil minerals composition, initial forest floor and soil organic pools, and C:N ratios. The model treats decomposition as a three-stage process (litter passes into fine litter and then through two successive soil organic fractions) during which nutrients are released from litter at rates depending on litterfall inputs and C:N ratios of litter and microbes.

The **NuCM** model has been calibrated for both a *Pinus taeda* L. site at Duke University (Johnson et al. 1995) and a mixed deciduous site at Walker Branch, Tennessee (Johnson et al. 1998b), which were selected for the following simulations because of their proximity to ongoing free-air carbon dioxide enrichment (FACE) studies. Because **NuCM** incorporates no physiological mechanisms, the effects of elevated CO_2 on nutrient cycling were examined by making appropriate modifications to N cycling parameters including: increased target growth; reduced foliar N concentration; reduced wood N concentration; and increased litter N mineralization.

Several features of **NuCM** should be noted with respect to the simulations described. First, vegetation biomass increment in the model will match the target growth rate input by the user only if no nutrient limitations develop. Both of the sites simulated are N-limited and simulated growth rates therefore fall well below expected optimal values in the base case (Johnson et al. 1995, 1998b). Second, **NuCM** includes an algorithm that allows increased or decreased vegetation nutrient concentrations according to nutrient supply. This allows the vegetation to continue to produce greater biomass per unit nutrient uptake (biomass/nutrient) when nutrients become limiting and also allows luxury consumption (increased nutrient/biomass) when nutrients are in excess. Menus allow the user to specify the percentage by which tissue stoichiometry is allowed to vary with respect to individual nutrients. Third, **NuCM** contains an algorithm for translocation (removal of nutrients from foliage before senescence) for deciduous (but not coniferous) species. Menus allow the user to specify the percentage of translocation that is allowed for each nutrient. However, translocation is not allowed for coniferous species, a point omitted from the **NuCM** user's manual (**NuCM** Code Version 2.0: An IBM PC

code for simulating nutrient cycling in forest ecosystems. Tetra-Tech, Inc. Hadley, MA), an oversight noted by Kvindesland (1997).

Hypotheses tested

Four hypotheses were explored with **NuCM**:

- (1) N limitations will preclude growth increases in response to elevated CO_2 in the absence of increases in N availability;
- (2) reductions in foliar N will cause increased biomass/N and temporarily increased growth; this will be reversed as increased litter C:N slows decomposition and reduces N availability;
- (3) reduced wood N concentration will cause increased biomass production per unit N uptake and, consequently, increased growth; and
- (4) increases in N mineralization will temporarily increase N cycling and growth, but the effect will diminish over time as the system re-equilibrates.

These hypotheses were examined by applying five scenarios to both the Walker Branch and Duke University sites: (1) no change; (2) increasing target growth and litterfall by 40% (+40% NPP); (3) reducing foliar N concentration by 40% (-40% Foliar N); (4) reducing wood N concentration by 40% (-40% Wood N); and (5) increasing litter N mineralization by 40% (+40% N Min). The simulations were run twice for the Walker Branch site, once with the measured rate of N translocation (47%, WBS-T; Johnson and Van Hook 1989) and once with no translocation (WBS-NT).

The simulations explore two ways in which N-limited systems could respond to elevated CO_2 : (1) increased biomass/N (reduced concentration); and (2) increased N mineralization. With respect to the first response, there is the added factor of negative feedbacks through the litterfall-decomposition pathway when foliar N concentration is reduced, but this is not a factor when woody N concentration is reduced. Hypotheses 2-4 consider all of these issues, whereas Hypothesis 1 considers the premise that N limitation actually precludes a growth response in the absence of a change in N cycling.

Results

Pinus taeda site

Hypothesis 1 was only partially supported in the Duke University simulations. Increasing target growth and litterfall (+40% NPP) caused increases in growth, vegetation N content and vegetation N increment between Years 1 and 5 compared to the Base scenario. This was followed by a decline to values well below the Base scenario in later years (Figures 1 and 2; Table 1). This response coincided with a steep decline in N status between Years 1 and 6, as reflected in the litterfall N, N increment, and N uptake patterns in all scenarios (Figure 2). The +40% NPP scenario caused the expected increase in litterfall N compared to the Base scenario except for a brief crossover between Years 4 and 6 (Figure 2). This increased litterfall N, in turn, caused an increase in forest floor N and soil N (Figure 1 and Table 1), apparently at the expense of vegeta-

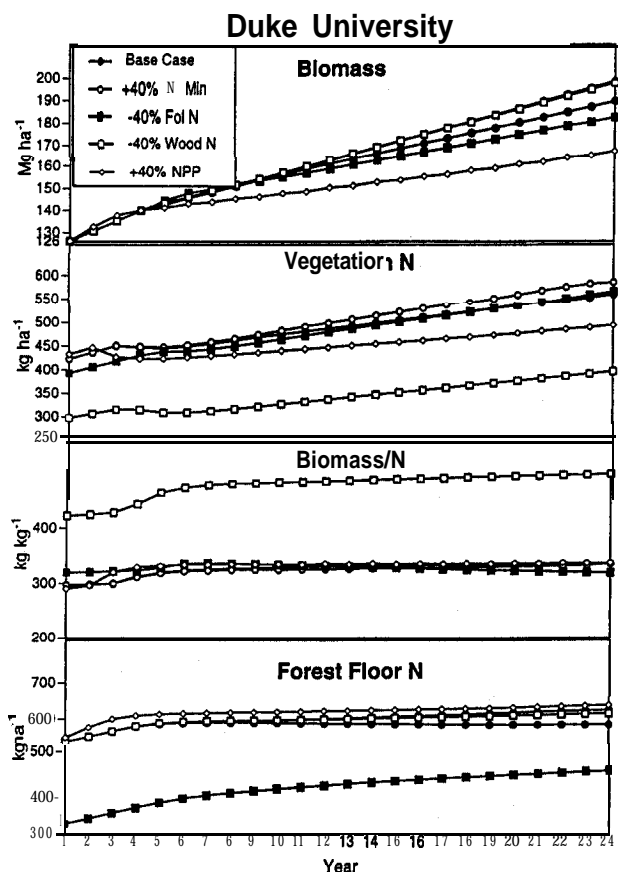


Figure 1. Biomass, vegetation N content, biomass per unit N content (biomass/N), and forest floor N content at Duke University, NC, simulated with NuCM. Scenarios include no change (Base), increasing N mineralization by 40% (+40% N Min), reducing foliar N concentration by 40% (-40% Foliar N), reducing wood N concentration by 40% (-40% Wood N), and increasing litterfall mass and target growth by 40% (+40% NPP).

tion N increment (Figure 2 and Table 1). Leaching of N was slightly lower in the +40% NPP scenario than in the Base scenario because of greater N immobilization in forest floor and soil.

Hypothesis 2 was supported in the Duke University simulations. Biomass in the -40% Foliar N scenario increased slightly compared to the Base scenario between Years 4 and 9, and this was followed by a decrease relative to the Base scenario in later years (Figure 1). Litterfall N was considerably lower in the -40% Foliar N scenario than in the Base scenario, as expected, and this allowed some additional available N to be allocated to woody increment (Figure 2); however, the reduction in litterfall was outweighed by the increase in increment, and thus N uptake was reduced compared to the Base scenario. Despite the greatly reduced litterfall N flux in the -40% Foliar N scenario, reduced decomposition, as a result of reduced litter C:N ratio, caused increased forest floor N increment compared to the Base scenario (Figures 1 and 2; Table 1). Because reduced decomposition in the -40% Foliar N scenario also caused less N input to the soil, N increment in the soil was

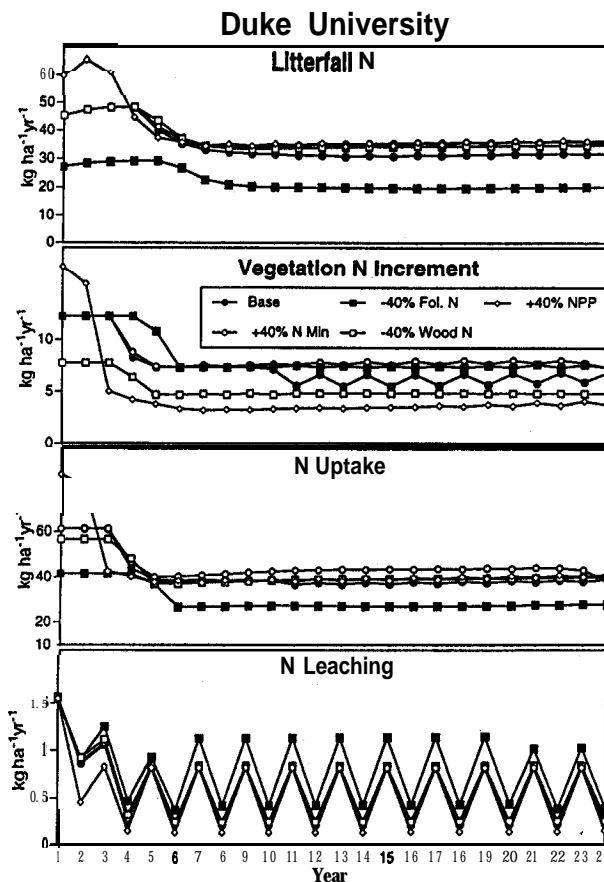


Figure 2. Nitrogen fluxes by litterfall, vegetation increment, uptake, and leaching at Duke University, NC, simulated with NuCM. Scenarios include no change (Base), increasing N mineralization by 40% (+40% N Min), reducing foliar N concentration by 40% (-40% Foliar N), reducing wood N concentration by 40% (-40% Wood N), and increasing litterfall mass and target growth by 40% (+40% NPP).

less than in the Base scenario (Table 1).

Hypothesis 3 was supported in the Duke University simulations. Reduced wood N concentration (-40% Wood N) caused greater biomass, reduced vegetation N content, and greater biomass/N than in the Base scenario (Figures 1 and 2). Total nitrogen uptake was reduced; however, the increase in biomass did not offset the reduction in wood N concentration. Nitrogen not taken up by the vegetation in the -40% Wood N scenario was not leached (leaching was similar to that in the Base scenario) but was accumulated in forest floor litter and soil (Table 1).

Hypothesis 4 was not supported by the Duke University simulations. Increased N mineralization (+40% N Min) caused greater biomass and vegetation N content than in the Base scenario and these differences increased over time (Figure 1). As expected, increments in soil N were reduced in the +40% N Mineralization scenario, but forest floor N pools increased, apparently because of greater litterfall N input (Figure 2 and Table 1). Increased N mineralization had only a slight effect on N leaching (14.9 compared to 14.3 kg ha⁻² in the Base scenario) (Figure 2 and Table 1).

Table 1. Simulated biomass and N increments (kg ha^{-1}) between Years 1 and 24 and leaching fluxes over 24 years.

Component	Base	+40% N Min	-40% Foliar N	-40% Wood N	+40% NPP
<i>Duke</i>					
Biomass	63	72	56	71	41
Vegetation N	176	200	201	126	112
Biomass/N	3.58	360	278	563	366
Forest Floor N	45	83	133	74	85
Soil N	225	137	98	232	240
Leaching	14.3	14.9	19.3	14.9	12.7
<i>Walker Branch with 47% translocation</i>					
Biomass	42	41	39	46	45
Vegetation N	110	106	101	83	116
Biomass/N	381	387	386	495	387
Forest Floor N	86	77	91	97	97
Soil N	-42	-26	-36	-39	-47
Leaching	16.9	16.7	15.1	17.1	13.6
<i>Walker Branch with 0% translocation</i>					
Biomass	8	9	8	9	4
Vegetation N	21	24	23	17	9
Biomass/N	381	375	348	529	444
Forest Floor N	86	94	127	88	98
Soil N	47	30	12	48	59
Leaching	0.25	0.32	0.25	0.35	0.07

Walker Branch mixed deciduous site with translocation (WBS-T)

Hypothesis 1 was only partially supported by the Walker Branch simulation with translocation (47% N translocation). Growth was slightly greater in the +40% NPP than in the Base scenario even though vegetation N content and uptake were nearly identical (Figures 3 and 4; Table 1). Forest floor N accumulated at a greater rate in the +40% NPP scenario than in the Base scenario, but soil N increment in this and all other scenarios was negative.

Hypothesis 2 was not supported in the Walker Branch simulations. Reduced foliar N caused slightly reduced growth throughout the simulation even though biomass/N was greater (Figure 3). In the -40% Foliar N scenario, forest floor N started at a lower value than in the Base scenario because of the lower litterfall N return (for the reasons previously described), but forest floor N increment was slightly greater than in the Base scenario because of reduced decomposition rate (Figure 4 and Table 1).

Hypothesis 3 was supported in the Walker Branch simulations. The reduced wood N concentration (-40% Wood N) scenario caused slightly increased biomass, slightly reduced vegetation N content, greatly reduced N increment, and greatly increased biomass/N compared to the Base scenario (Figures 3 and 4). Only a small amount of the N not taken up by the vegetation in this scenario leached (17.1 compared to 16.9 kg ha^{-1} in the Base scenario) (Figure 4 and Table 1).

Hypothesis 4 was not supported by the Walker Branch simulations. Biomass and vegetation N were slightly decreased in the +40% N Min scenario compared to the Base

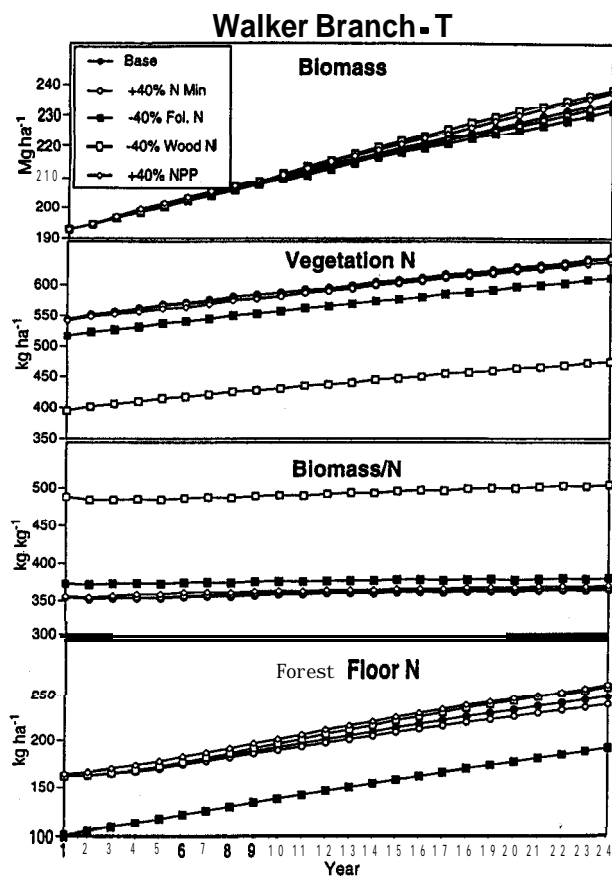


Figure 3. Biomass, vegetation N content, biomass per unit N content (biomass/N), and forest floor N content at Walker Branch, TN, simulated with NuCM. Translocation is set at 47%. Scenarios include no change (Base), increasing N mineralization by 40% (+40% N Min), reducing foliar N concentration by 40% (-40% Fol. N), reducing wood N concentration by 40% (-40% Wood N), and increasing litterfall mass and target growth by 40% (+40% NPP).

scenario (Figure 3 and Table 1). Compared with the Base scenario, forest floor N was reduced and soil N became less negative in the +40% N Min scenario, but litterfall, increment, uptake and leaching were only slightly affected (Figures 3 and 4; Table 1).

Walker Branch mixed deciduous site without translocation (WBS-NT)

Setting translocation to 0% at Walker Branch caused major changes in simulated growth and N cycling. Litterfall N in the WBS-NT scenarios was greater than in the WBS-T scenarios (e.g., 32-34 versus 19-20 $\text{kg ha}^{-1} \text{ year}^{-1}$ in the respective Base scenarios) (Figures 4 and 5). In turn, the increase in litterfall N caused greater forest floor N mass in the WBS-NT simulations than in the WBS-T scenarios (170-256 versus 162-248 kg ha^{-1} in the respective Base scenarios) (Figures 4 and 5), but no difference in the net increment to the forest floor (86 kg ha^{-1} in the Base scenarios in each case; Table 1). Soil N increment became positive in the WBS-NT simulations, apparently because of greater litterfall N input. Growth, vegetation N up-

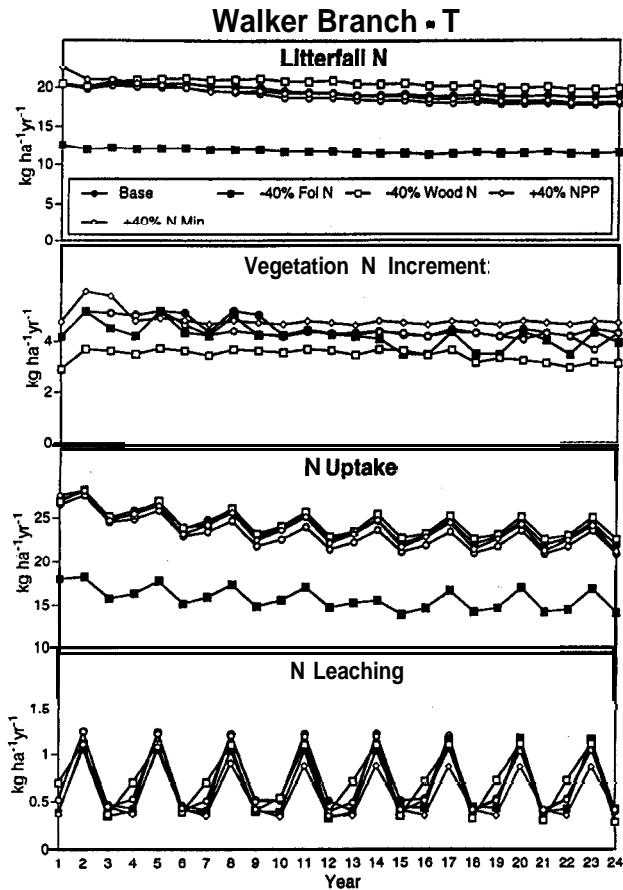


Figure 4. Nitrogen fluxes via litterfall, vegetation increment, uptake, and leaching at Walker Branch, TN, simulated with NuCM. Translocation is set at 47%. Scenarios include no change (Base), increasing N mineralization by 40% (+40% N Min), reducing foliar N concentration by 40% (-40% Foliar N), reducing wood N concentration by 40% (-40% Wood N), and increasing litterfall mass and target growth by 40% (+40% NPP).

take, N increment, and leaching were greatly reduced in the WBS-NT scenarios compared to the WBS-T scenarios, because of greater soil N increment and greater allocation of N away from wood increment to litterfall (Figures 5 and 6; Table 1).

The responses at the Walker Branch site to the various scenarios also changed significantly when translocation was set to zero. In contrast to the results from the WBS-T simulations, Hypothesis 1 was supported in the WBS-NT simulations: the +40% NPP scenario had a negative effect on biomass, vegetation N content, and vegetation N increment (Figures 5 and 6). The increments of N in the forest floor (98 kg ha⁻¹) was nearly identical to that in the WBS-T simulation (97 kg ha⁻¹), but the increment in soil N was considerably greater (+59 versus -47 kg ha⁻¹) (Table 1).

In contrast to the WBS-T simulations, the -40% Foliar N scenario in the WBS-NT simulations caused slightly increased growth, reduced vegetation N, and increased biomass/N compared to the Base scenario (Figures 5 and 6). Litterfall N was considerably lower in the -40% Foliar N scenario than in the

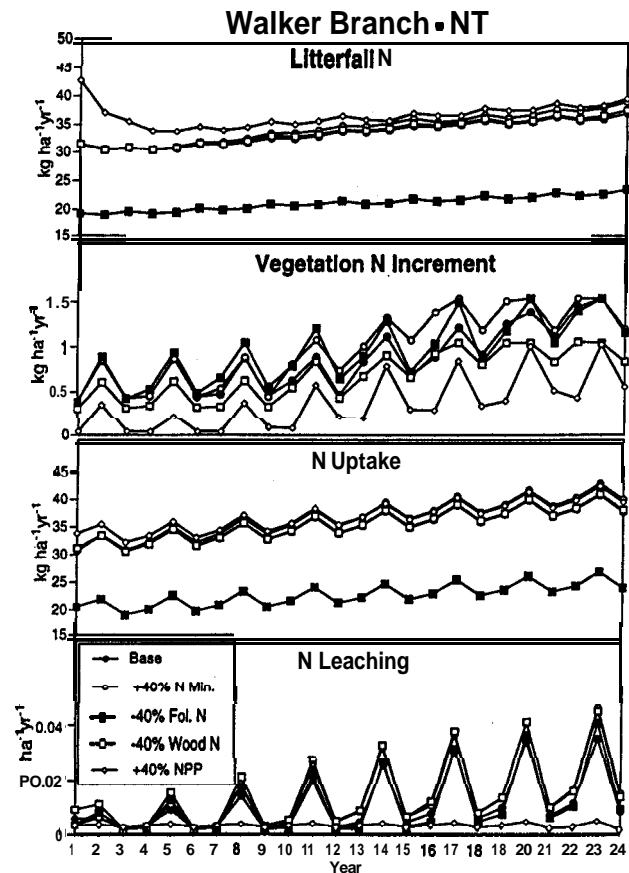


Figure 5. Nitrogen fluxes via litterfall, vegetation increment, uptake, and leaching at Walker Branch, TN, simulated with NuCM. Translocation is set at 0%. Scenarios include no change (Base), increasing N mineralization by 40% (+40% N Min), reducing foliar N concentration by 40% (-40% Foliar N), reducing wood N concentration by 40% (-40% Wood N), and increasing litterfall mass and target growth by 40% (+40% NPP).

Base scenario, as expected, allowing a greater proportion of available N to be incorporated into woody tissue (greater increment) (Figure 5). However, the increase in N increment did not offset the reduced litterfall N, because N uptake was greatly reduced in the -40% Foliar N scenario compared to the Base scenario (Figure 5). Forest floor N increment in the -40% Foliar N scenario (127 kg ha⁻¹) was greater than in the Base scenario (86 kg ha⁻¹) and greater than in the WBS-T, -40% Foliar N scenario (91 kg ha⁻¹). Soil N increment in the -40% Foliar N scenario was less than in the Base scenario because of reduced N input from more slowly decomposing litter.

Hypothesis 3 was supported in the WBS-NT simulations as in the WBS-T simulations. The reduced wood N concentration (-40% Wood N) scenario caused increased biomass, reduced vegetation N content and N increment and greatly increased biomass/N compared to the Base scenario (Figures 5 and 6). Only a small amount of the N not taken up by the vegetation in this scenario leached (0.35 kg ha⁻¹ compared to 0.25 kg ha⁻¹ in the Base scenario) (Figure 5 and Table 1).

In contrast to the WBS-T simulation but similar to the Duke

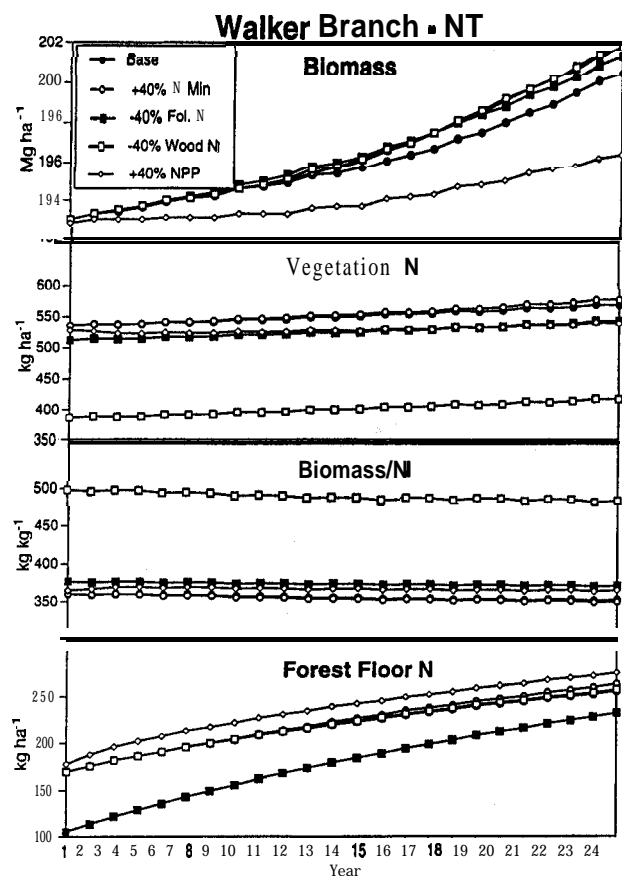


Figure 6. Biomass, vegetation N content, biomass per unit N content (biomass/N), and forest floor N content at Walker Branch, TN, simulated with NuCM. Translocation is set at 0%. Scenarios include no change (Base), increasing N mineralization by 40% (+40% N Min), reducing foliar N concentration by 40% (-40% Foliar N), reducing wood N concentration by 40% (-40% Wood N), and increasing litterfall mass and target growth by 40% (+40% NPP).

University simulation, the +40% N Min scenario in the WBS-NT simulation caused slightly increased biomass and vegetation N compared to the Base scenario (Figure 6 and Table 1). As in the Duke University simulation, this pattern did not decrease over time, but continued throughout the 24-year simulation. Also, as in the Duke University simulation, soil N increment was reduced in the +40% N Min scenario, but forest floor N increment increased (Figure 5 and Table 1). Leaching was only slightly increased with increased N mineralization compared with the Base scenario (0.32 versus 0.25 kg ha^{-1}) (Figure 5 and Table 1).

Discussion

The simulations suggest that reducing foliar N concentrations will not allow prolonged responses to elevated CO_2 because of negative feedbacks in the biogeochemical N cycle (i.e., reduced litter C:N ratio, reduced decomposition and N immobilization in forest floor). These effects were most pronounced at the Duke University site, where the forest floor N content was

higher and N turnover rate was lower than at the Walker Branch site. Reducing wood N concentration, on the other hand, allowed prolonged increases in growth in response to elevated CO_2 because of greater biomass/N without any significant slowing of the biogeochemical N cycle.

The -40% Wood N simulations illustrate the difficulties associated with using the term "nutrient-use efficiency" to describe the phenomenon of reduced concentration (or increased biomass/N). In this case, the vegetation was actually less "efficient" in taking up N and allowed more N to accumulate in the forest floor than in the Base scenario. Thus, a more precise term such as reduced concentration or increased biomass/N to describe this effect is desirable.

In a more general sense, these simulations suggest that the allocation of a limiting nutrient (like N) between litterfall and wood increment strongly affects overall N cycling and growth. The simulation results pose the counterintuitive hypothesis that increased biogeochemical cycling of N (through increased litterfall N) will cause reduced growth in an N-limited system. The reduction in growth in the Duke University +40% NPP scenario was a result of increased allocation of N to litterfall, leading to an increased accumulation of N in the forest floor and soil. Given that the system is N-limited, N uptake and growth are constrained by the supply of available N from atmospheric deposition and soil N mineralization. Thus, forcing more N allocation to litterfall (as was done in these simulations) automatically reduces the amount of N that can be incorporated into woody tissue, and this reduces growth. Translocation allows the trees to retain a greater proportion of N taken up, rather than recycle it back to the forest floor and soil where it can be immobilized. Translocation in the Walker Branch scenarios allowed the allocation of N between litterfall and increment to remain stable, even when litterfall mass was increased in the +40% NPP scenario, and this allowed greater N availability and vegetation growth. When translocation was eliminated in the Walker Branch simulations, growth was reduced because of increased allocation to litterfall, as in the Duke University simulations.

The Walker Branch simulations suggest that translocation is of major importance in N cycling in the Walker Branch system. In three of the four scenarios simulated, setting translocation to zero changed the direction as well as the magnitude of the responses. It seems probable that varying translocation rates between 0 and the observed 47% or higher will also have major effects on simulated N cycling in this system. Such simulations are now being planned.

The effects of translocation on N cycling in the Duke University simulations are not known, because translocation has to be set to zero for conifers in the current version of NuCM. Cole and Rapp (1981) found that, on average, translocation in coniferous forests is approximately 0 (i.e., the N requirement for new growth is approximately equal to N uptake); however, Johnson and Lindberg (1991) estimated that N translocation for the Duke University forest was 66%. Thus, the effects of translocation on N cycling in the Duke University forest need to be investigated.

Acknowledgments

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